

SCALE-DEPENDENT HABITAT SELECTION BY AMERICAN REDSTARTS IN ASPEN-DOMINATED FOREST FRAGMENTS

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ABSTRACT.—We examined scale-dependent site occupancy of American Redstarts (*Setophaga ruticilla*) in forest fragments (2–140 ha in area) dominated by mature trembling aspen (*Populus tremuloides*) in central Alberta, Canada. Vegetation within territories, both adjacent to and away from nests, differed from vegetation in unoccupied fragments and within occupied fragments outside of territories. Territories contained higher densities of willow (*Salix* sp.), a taller shrub-layer, and lower densities of trembling aspen than other sites. Willow was the most frequently used plant species for nesting and foraging. Our results indicate that even within mature forest patches, American Redstarts select disturbed areas dominated by early successional plant species. Received 6 March 1998, accepted 30 Aug. 1998.

Numerous researchers have investigated habitat selection by American Redstarts (*Setophaga ruticilla*), but debate continues regarding the preferred age of forest stands used for breeding. Although most studies reported that American Redstarts prefer early successional forests (Martin 1960, Collins et al. 1982, DeGraaf 1991, Westworth and Telfer 1993, Huffman 1997), they have also been commonly found in mid- to late successional stands (Bond 1957, Ficken and Ficken 1967, Crawford et al. 1981, Morgan and Freedman 1986, Thompson and Capen 1988). Scale-dependent habitat requirements have been poorly documented for the American Redstart. Because abiotic and biotic factors may affect a species differently at various spatial scales (Bock 1987, Wiens et al. 1987), some documented differences in habitat selection may be due to scale effects. Thus, a holistic understanding of a species' habitat use patterns may require that data be collected and analyzed at several spatial scales (e.g., patch, territory, and nest site; Bergin 1992, Steele 1992, Kelly 1993). Considering that many forest patches are heterogeneous in age and structure (e.g., woody vegetation may increase in age and height from edge to interior), the investigation of scale-dependent habitat use patterns of the American Redstart could clarify the species' requirements and reconcile some of the inconsistencies in reported habitat preferences.

We studied scale-dependent habitat selection of the American Redstart in forest fragments dominated by mature trembling aspen (*Populus tremuloides*) at the northwestern edge of the species' range in central Alberta, Canada. We asked: (1) do American Redstarts occupy available forest fragments based on particular habitat characteristics (vegetation structure and composition), and (2) within an occupied fragment, do American Redstarts select territories and nest sites based on habitat characteristics?

STUDY AREA AND METHODS

The study was conducted around the Meanook Biological Research Station (54° 37' N, 113° 20' W) near Athabasca, Alberta, between 9 May and 6 July 1994. Upland forests in this region are primarily a mosaic of trembling aspen and white spruce (*Picea glauca*) stands which was historically created and maintained by fire (Rowe 1972). We examined eight forest fragments dominated by mature (>80 yr old) trembling aspen interspersed with patches of willow (*Salix* sp.) and alder (*Alnus* spp.). A fragment was defined as a wooded area separated from other wooded areas by more than 30 m of cropland or pasture (see Villard et al. 1995). Forest fragments varied from 2 to 140 ha (areas were calculated from 1:30,000 aerial photographs using a Placon® digital planimeter). All fragments were located within a 9-km² area and represented the range of fragment sizes available in the landscape (for details see Sodhi and Paszkowski 1997). The selection of fragments was constrained by various factors including stand age, access, presence of cattle, and landowner cooperation.

Each fragment was flagged into 100 × 100 m grids and was surveyed three times to locate redstart territories. During surveys, we walked along the flagged gridlines and visually located all redstarts (primarily by following singing males). Locations of redstarts, along with characterization of individual plumage patterns (see below) were recorded on a gridded map.

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Unoccupied fragments were surveyed again in late June by playing American Redstart territorial songs for 2 min at 50-m intervals and waiting 5 min for a response. No new individuals were detected during these surveys. Individual males were identified based on location of territory and on patterns of plumage coloration on the breast, abdomen, neck, and head (Sherry and Holmes 1989, Lemon et al. 1992). Because second year male redstarts can differ from older males in habitat selection (e.g., Sherry and Holmes 1989, Hunt 1996), we collected habitat data only for males in full adult plumage.

The composition of vegetation was measured within territories, outside of territories, adjacent to the nest tree, and in unoccupied habitat fragments. We sampled in early to mid-July after the breeding season. Vegetation plots were located at random with the following exceptions: plots associated with nest trees were dictated by nest location and plots associated with territories were always placed at least 10 m inside a boundary. A total of 88 vegetation plots were sampled: 33 within 13 territories, 17 outside of territories but within 4 occupied fragments, 17 immediately around 17 nest trees, and 21 plots in 4 unoccupied fragments.

We sampled vegetation using a modification of the circular sample-plot method (James and Shugart 1970). For each of the four site types, we recorded four sets of information: (1) tree (woody plants more than 1.75 m tall) species, number, height (using a clinometer), and diameter at breast height (using a dbh measuring tape) within a 22.4 m diameter circular plot, (2) shrub (woody plant less than 1.75 m tall) species, number, and maximum height within a 10 m diameter circular plot, (3) presence/absence of canopy (above 5 m) at 20 random points within the 22.4 m diameter plot using a 4 cm diameter ocular tube, and (4) presence/absence of ground cover at the same 20 random points using the ocular tube. The last two sets of information gave a measure of relative canopy and ground cover, respectively.

We used Principal Components Analysis (PCA) to compare vegetation composition within and among the four site-types (CANOCO; ter Braak 1991) for all 88 plots. Principal Components Analysis is recommended and frequently used for analysis of habitat data (Doncaster et al. 1996, Hunt 1996). The 27 vegetation variables recorded for each plot (Table 1) were square-root transformed to approximate a normal distribution. A univariate analysis, Kruskal-Wallis test, was used to determine if PCA scores for the first two ordination axes differed among site types. If the Kruskal-Wallis test was significant ($P < 0.05$), Multiple Comparisons tests were performed to determine which characteristics differed (Siegel and Castellan 1988). All statistical tests were done using STATVIEW version 4.1 on a Macintosh-compatible computer.

RESULTS

Redstarts occurred in four forest fragments (2, 50, 107 and 140 ha in area) but were ab-

sent from four others (4, 6, 9 and 32 ha). Principal Components Analysis based on vegetation characteristics clearly grouped and separated unoccupied plots from plots within territories (Fig. 1). Loadings of vegetation variables on PCA Axis I indicated that unoccupied fragments and areas outside of territories within occupied fragments contained larger trees and higher densities of trembling aspen, accompanied by prickly wild rose (*Rosa acicularis*), red-osier dogwood (*Cornus stolonifera*), and honeysuckle (*Lonicera* spp.) (Table 1). Areas within territories were characterized by high densities of willow (both trees and saplings), cherry (*Prunus* sp.), saskatoon berry (*Amelanchier alnifolia*) and balsam poplar (*Populus balsamifera*) saplings, as well a tall shrub-layer (loadings on Axis 1, Table 1). Scores on Axis I differed significantly among site types ($KW = 42.51$, $df = 3$, $P < 0.001$). There was no significant difference between nest sites and plots within territories (Multiple Comparisons test: $P > 0.05$), but both differed significantly from plots in unoccupied fragments and plots outside of territories within occupied fragments (Multiple Comparisons tests: $P < 0.05$). Plots in unoccupied fragments and those outside of territories in occupied fragments had similar PCA I scores (Multiple Comparisons test: $P > 0.05$).

Nest sites were associated with high densities of white birch (*Betula papyrifera*, both trees and saplings), willow, cherry, and balsam poplar saplings, as well as *Viburnum* spp., which contributed to a tall shrub layer (high scores and loadings on Axis II). Nest sites were also clustered on PCA Axis II ($KW = 17.79$, $df = 3$, $P < 0.001$). On this axis, only scores for nest sites differed significantly from scores for plots from unoccupied fragments (Multiple Comparisons tests, $P < 0.05$). However, there was similarity in vegetation characteristics in some plots within territories and those at nest sites (Fig. 1).

DISCUSSION

Principal Components Analysis and subsequent univariate analyses indicate that redstarts did not establish territories randomly within or among forest patches, but based their occupancy on vegetation characteristics. A high abundance of willow was a particular-

TABLE 1. Loadings of vegetation variables on the first and second Principal Components axes (PC I and PC II).

Variables	PC I	PC II
Eigenvalues	0.42	0.12
Variation explained (%)	42.4	11.1
No. trees (woody plants > 1.75 m tall)		
Willow (<i>Salix</i> sp.)	-121	-289
Trembling aspen (<i>Populus tremuloides</i>)	338	-654
Balsam poplar (<i>P. balsamifera</i>)	38	19
White birch (<i>Betula papyrifera</i>)	-101	556
Alder (<i>Alnus</i> spp.)	29	195
White spruce (<i>Picea glauca</i>)	28	133
Tree sizes		
Mean tree height (m)	-95	-68
Mean dbh (mm)	203	318
No. shrubs (woody plants 0.5–1.75 m tall)		
Red-osier dogwood (<i>Cornus stolonifera</i>)	224	106
Wild gooseberry (<i>Ribes oxycanthoides</i>)	-55	103
Wild red raspberry (<i>Rubus idaeus</i>)	75	-229
Honeysuckle (<i>Lonicera</i> spp.)	183	-418
Prickly wild rose (<i>Rosa acicularis</i>)	996	81
Snowberry (<i>Symphoricarpos</i> spp.)	203	88
<i>Caragana</i> sp.	-74	-121
<i>Viburnum</i> spp.	91	522
<i>Prunus</i> spp.	-223	448
Saskatoon berry (<i>Amelanchier alnifolia</i>)	-139	-5
Maple sapling (<i>Acer</i> sp.)	-11	0
Balsam poplar sapling	-122	266
Willow sapling	-158	380
Trembling aspen sapling	39	196
White birch sapling	-119	769
Alder sapling	142	172
Shrub height		
Mean maximum shrub height (mm)	-206	563
Cover ^a		
Canopy	-97	177
Ground	-37	5

^a See Methods for estimation of these variables.

ly distinctive feature of areas within territories and around nest sites. Willow was the most frequently used foraging site (mean \pm SE = $65.8 \pm 8.9\%$ of observation time, $n = 13$ males for which we had at least 10 min of observations) and nesting site (13 of 20 nests; Sodhi and Paszkowski, unpubl. data). Areas within territories and nest sites were characterized not only by willows, but also by a tall shrub layer in general. American Redstarts have been found to be positively associated with shrub cover in Minnesota (Huffman 1997). The extra cover and structural complexity provided by taller shrubs may have protected nests from predation or parasitism and thus enhanced reproductive success (Mor-

ris and Lemon 1987). Nest sites also supported higher densities of white birches, which have wider leaves than willows and may improve nest cover. In our study area, only 18% ($n = 22$) of the nests were parasitized by Brown-headed Cowbirds (*Molothrus ater*) and only 18% ($n = 22$) were depredated (Sodhi and Paszkowski, unpubl. data). Both nest parasitism and depredation rates at our sites were relatively low compared to other studies (e.g., Freedman 1929, Sherry and Holmes 1992). The structural complexity of understory vegetation in earlier successional stages could offer appropriate nest protection for redstarts.

Certain plant species, most notably trembling aspen, were underrepresented on sites

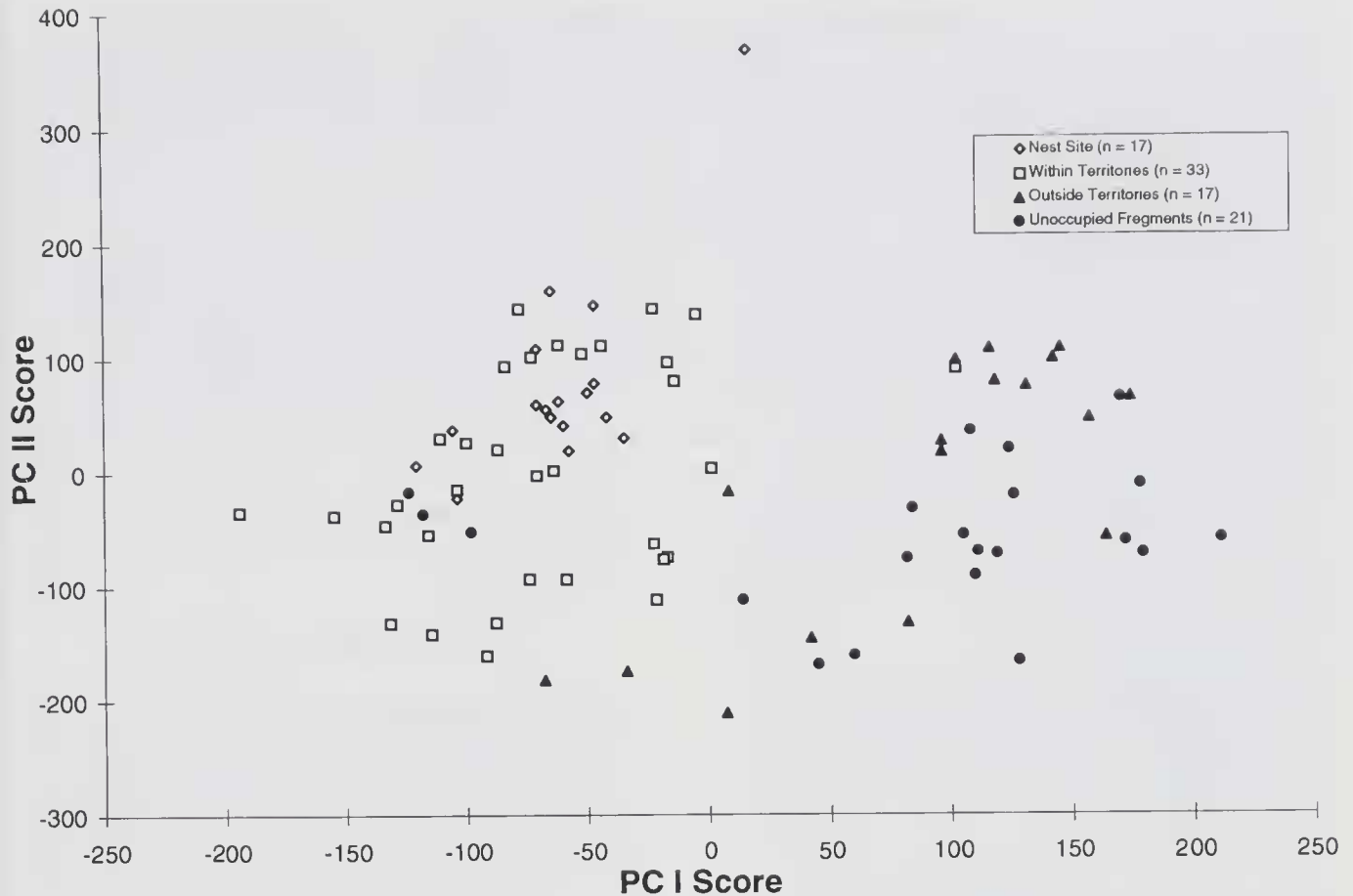


FIG. 1. Comparison of sites occupied and unoccupied by American Redstarts based on the first two Principal Component scores of plot vegetation. The Principal Components are based on 27 vegetation variables collected from 88 plots. Note: one plot near a nest was the only plot dominated by conifers and it contained little undergrowth, therefore it is distinct from all other plots.

occupied by redstarts. The lack of use of habitat dominated by common, and even dominant, tree and shrub species at both the scale of the forest patch and the territory may be related to constraints imposed on redstart foraging behavior by the leaf and branch morphology of these plant species (Holmes et al. 1978, Sedgewick and Knopf 1992). The exclusion and inclusion of certain shrub species on redstart territories could also be an artifact of their co-occurrence with overstory dominants, especially trembling aspen. The canopy forming woody species associated with habitat used by redstarts, i.e., willow and white birch, are all species typically found on wetter sites in central Alberta (Rowe 1972). Thus, it is also possible that redstarts were choosing locations in this relatively dry landscape that had higher soil moisture levels and were therefore more productive in terms of plant and invertebrate biomass (Adams and Morrison 1993). Our surveys showed that even within stands dominated by mature trembling

aspen, redstarts preferred areas that supported more willows, which are typically early successional species. The presence of thickets of willow and other shrubs in these stands might be maintained by periodic localized flooding resulting from vernal soil saturation following heavy snow cover or from beaver activity (Sodhi and Paszkowski, pers. obs.).

American Redstarts are abundant in harvested aspen forests in Minnesota (Hoffman 1997). Other studies also show that redstarts attain maximum densities in stands in early successional stages of different forest types (DeGraaf 1991, Westworth and Telfer 1993, Hunt 1996). It might be argued, based on patterns reported for some other passerines (Vickery et al. 1992), that although redstarts occur at high densities in early successional forests, they reproduce poorly here compared to mid- to late successional forests. We found that 90.6% ($n = 32$) of older adult redstart males were paired in our study area in 1994 (Sodhi, unpubl. data); this figure is similar to

values for older males in various successional forests and in a continuous forest tract in New Hampshire (Sherry and Holmes 1989, Hunt 1996). Assuming that male pairing success is correlated with reproductive success, pockets of disturbed, productive early successional vegetation nested within mature forest stands may offer good breeding conditions for redstarts.

Every avian habitat can be represented as a spatially based hierarchy that ranges from the level of landscape to nest site. The behavioral decision-making processes behind habitat use can be related to these hierarchical habitat units (Kolasa 1989, Kotliar and Wiens 1990). Studies of scale-dependent habitat selection have revealed that the decision-making process varies among species and can sometimes operate at multiple scales within a single species (Bergin 1992). For example, Black-throated Blue Warblers (*Dendroica caerulescens*) were more selective at the habitat patch (or stand) level than at the territory level (Steele 1992). In contrast, habitat selection in Dusky Flycatchers (*Empidonax oberholseri*) was primarily based on nest-site characteristics rather than on territorial features (Kelly 1993). In our study, habitat selection by American Redstarts operated most clearly at the territory level. Males defended areas of forest with a distinct plant composition and structure. Habitat selection at the territorial level was manifested, in turn, at the next higher spatial scale, as males did not occupy fragments that contained insufficient appropriate vegetation. At the finest spatial scale, evidence for nest site selection was present but relatively weak. Nest sites were not significantly different from other locations within territories, possibly because the willows and other tall shrubs used as foraging sites also offered good nest protection.

Some question remains as to whether birds actually differentiate between potential territories based on the environmental parameters that researchers perceive to be important (Morse 1989). Most authors agree however, that, at some level, territory establishment is a behavioral response to certain vegetation characteristics (Maurer and Whitmore 1981, Smith and Shugart 1987, Parrish and Sherry 1994). We concur that American Redstarts in central Alberta establish territories within a

definable type of vegetation that appears to offer appropriate conditions for successful foraging and nesting. Based on our research, as well as previous studies, redstarts appear to prefer early successional forest stands or disturbed sites embedded within older stands. However, with correlative data, it remains possible that redstarts choose sites based on soil moisture or food availability, which are in turn associated with particular vegetation characteristics. In light of reported population declines for the species in parts of its range (Sauer et al. 1996), the value of such habitats should be assessed on a regional basis and their use by redstarts integrated into conservation strategies.

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